

# Invariant scaling relations across tree-dominated communities

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**Organizing principles are needed to link organismal, community and ecosystem attributes across spatial and temporal scales. Here we extend allometric theory—how attributes of organisms change with variation in their size—and test its predictions against worldwide data sets for forest communities by quantifying the relationships among tree size–frequency distributions, standing biomass, species number and number of individuals per unit area. As predicted, except for the highest latitudes, the number of individuals scales as the  $-2$  power of basal stem diameter or as the  $-3/4$  power of above-ground biomass. Also as predicted, this scaling relationship varies little with species diversity, total standing biomass, latitude and geographic sampling area. A simulation model in which individuals allocate biomass to leaf, stem and reproduction, and compete for space and light obtains features identical to those of a community. In tandem with allometric theory, our results indicate that many macroecological features of communities may emerge from a few allometric principles operating at the level of the individual.**

Despite insights from ecological theory and experimental manipulation, mechanistic connections among important characteristics of ecological communities across diverse ecosystems have remained elusive<sup>1–7</sup>. Variation in species diversity has been explained in terms of a subdivision of community niche space with a presumed concomitant change in total standing biomass and productivity<sup>2,3,8,9</sup>. Yet, the ecological properties of communities or ecosystems accounting for this remain contentious<sup>2,5,10–13</sup>.

One promising mechanistic approach interrelating many organismal, community and ecosystem properties is to focus on size-dependent (allometric) relationships that demonstrably cut across phylogenetically disparate species<sup>6–7,14–25</sup>. One of the most prevalent allometric patterns observed for both plant and animal communities is the inverse relationship between body mass and abundance<sup>23,26,27</sup>. Because this relationship reflects how biomass and productivity are partitioned among individuals, it offers considerable insight into the mechanisms structuring ecological communities across varying environments. However, relatively little is known about how community size–frequency distributions vary across different environments or how they vary among communities differing in species composition. Here we provide a broad theoretical framework for the size–frequency distributions of plant communities. We also show how the allometric constraints on resource use and plant form influence many of the macroscopic properties of tree-dominated communities.

## Extending allometric theory to plant communities

Allometric theory<sup>16</sup> predicts that the total number of individuals,  $N$ , in any size class  $m$ , equals  $C_m M^{-3/4}$ , where  $C_m$  is the number of individuals per unit area normalized to a given size class  $m$ , and  $M$  is the total body mass in class  $m$ . This relationship is predicted to hold true when all available space is occupied such that the total rate of resource use of all individuals within a community  $Q_{\text{Tot}}$  (which is proportional to rates of gross primary production<sup>17</sup>) approximates the rate of resource supply from the environment  $R$  (that is,  $Q_{\text{Tot}} \approx R$ )<sup>16</sup>. Biomechanical and allometric theory<sup>14,15</sup> also predicts that  $M$  is proportional to the  $8/3$  power of stem diameter  $D$  of any size class (that is,  $M \propto D^{8/3}$ ), such that  $N$  will scale as  $N \propto M^{-3/4} \propto D^{-2}$ .

If these scaling laws hold for entire communities, organismal traits can be used to link to larger-scale properties of communities across different ecosystems. For example, extensions of allometric

and biomechanical theory predict that total standing community biomass will be invariant with respect to species composition and thus latitude. Furthermore, the intrinsic capacity to produce biomass on an annual basis will vary little across communities. Note that total standing community biomass,  $M_{\text{Tot}}$ , is given by the formula

$$M_{\text{Tot}} = C_m \int_a^b M^{-3/4} dM = 4C_m [M_a^{1/4} + M_b^{1/4}] \quad (1)$$

where the subscripts  $a$  and  $b$  denote maximum and minimum body mass within a given community, respectively. As both the minimum and maximum body sizes are largely insensitive to species composition or latitude<sup>14</sup> (see also results below), any variation in  $M_{\text{Tot}}$  will be determined by variation in  $C_m$ . For closed canopy forest, however, both theory and observation suggest that  $C_m$  varies little, such that  $M_{\text{Tot}}$  is expected to vary little across communities.

Specifically, for any given size class,  $R_m \approx Q_m \approx C_m B_m$ , where the metabolic rate  $B_m = C_B A_m$ . Here,  $A_m$  is leaf or root area, and  $C_B$  is the rate of resource use per unit area, which can vary across species. Because allometric theory and empirical data<sup>14,16–18</sup> show that  $A_m = C_A (M/\rho)^{3/4}$ , where  $\rho$  is the bulk tissue density and  $C_A$  is a constant of proportionality reflecting the species-specific amount of leaves or roots per individual per unit area, we derive the formula

$$C_m \approx \frac{R_m}{C_A C_B (M_m/\rho)^{3/4}} \quad (2)$$

which quantitatively shows how numerous factors can influence plant population density per size class. Nonetheless, biometric and physiological data indicate no significant differences in the mean values of  $C_B$ ,  $C_A$  and  $\rho$  across tropical and temperate tree species or with variation in species richness<sup>16,17,20–22</sup> (see also Methods). This invariance indicates that total community biomass is likely to be insensitive to species diversity, even though  $C_m$  can vary because of the many environmental factors (such as temperature and precipitation) known to influence  $R_m$ .

Variation in species diversity might also independently influence  $R_m$ , the quantity of resources used per size class per unit time. In particular, variation in  $R_m$  might result either from an increase in total niche volume occupied or as a consequence of synergistic effects from increased diversity such as overyielding<sup>10–11,13</sup>, both of which can influence the total number of individuals across size classes and thus alter total community biomass<sup>4</sup>. A full treatment of

ontogenetic growth is complicated; however, empirical and theoretical data for plants, spanning 20 orders of magnitude in size (unicellular algae to trees), indicate that short-term rates of biomass production per individual,  $G$ , which approximates the whole-organism metabolic rate,  $B$ , scales as  $G \approx B \propto M^{3/4}$  (refs 17, 18, 25). Thus, interspecific rates of biomass production are predicted to be intrinsically equivalent in relation to size within and across plant communities.

As the total rate of community resource use  $R_{Tot} \propto NQ \propto NB \approx G_{Tot}$ , where  $G_{Tot}$  is the net primary production of biomass of a given community, it follows that  $G_{Tot} \approx QN \propto M^{3/4}M^{-3/4} \propto M^0$  (ref. 16). This equation predicts that rates of production both within and across communities are invariant with plant size. Furthermore, if  $C_m$ ,  $M_a$  and  $M_b$  (from equation (1)) do not vary across communities, then it also follows that variation in rates of plant community total biomass production,  $G_{Tot}$ , are more influenced by ecological factors that reduce the capacity of metabolic production<sup>6</sup> (for example, abiotic and biotic features of ecosystems which influence the extent to which plants can maximally transpire water and assimilate  $CO_2$ ) than by species-specific physiological capacities or variation in species diversity.

**Empirical validation of allometric theory**

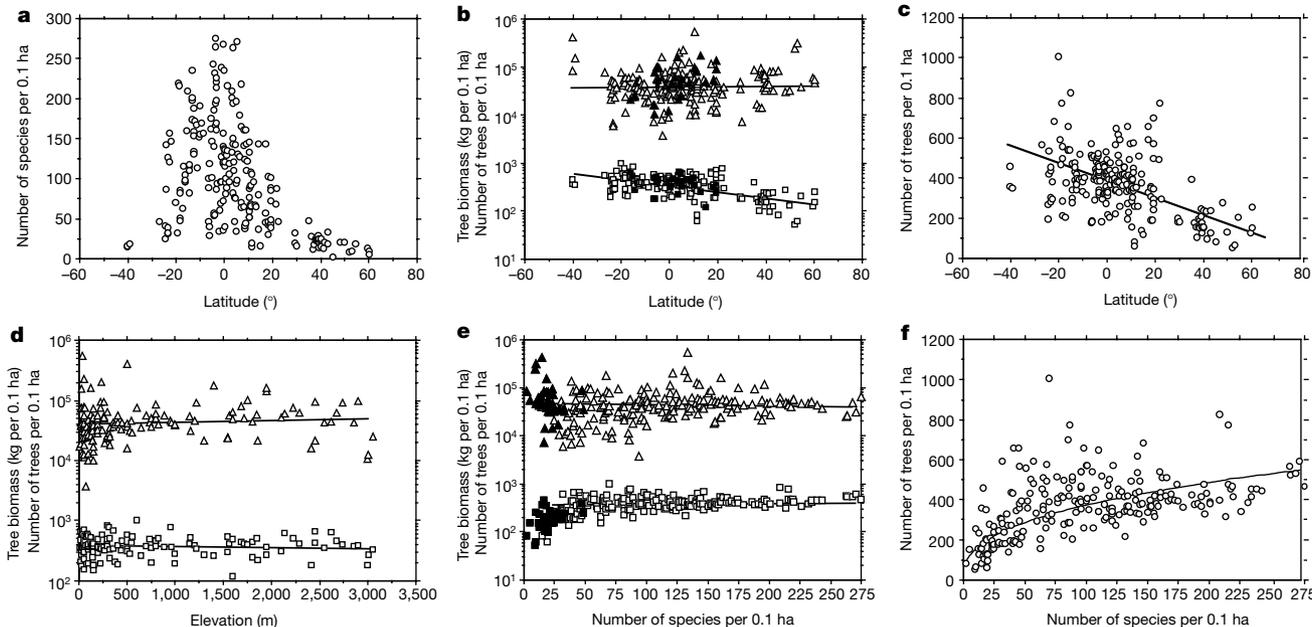
Clearly, these predictions, which follow directly from biophysical first principles dictating size-dependent optimal biomass allocation patterns<sup>14–17</sup>, require empirical verification. Here we test these predictions on the basis of macroecological data sets that span taxonomically and physiognomically diverse plant communities. We primarily draw on a large data set assembled by Gentry<sup>28,29</sup>, which spans near-monospecific stands to some of the most bio-

diverse forested communities on Earth. Specifically, the Gentry data set represents a 22-year accumulation from 227 sites across 6 continents of tropical and temperate closed-canopy forest communities ranging from 60.4°N to 40.43°S latitude and from 20 to 3,050 m in elevation.

In each site sampled, all plants, including lianas with stem diameters  $\approx 2.5$  cm measured at breast height (d.b.h.), were sampled along ten 2×50-m transects, totalling 0.1 ha at each site. Species numbers and numbers of individuals per site are in the ranges 2–275 and 52–1,005, respectively. The complete data set contains 83,121 individual plants (maximum d.b.h. ranges between 26 and 412 cm). (Information and access to the data are available at [http://www.mobot.org/MOBOT/Research/applied\\_research/gentry.html](http://www.mobot.org/MOBOT/Research/applied_research/gentry.html); see also Supplementary Information.)

**Results**

On the basis of the above protocol, the maximum number of species per 0.1 ha increases toward the equator (Fig. 1a). Yet, total tree standing biomass per 0.1 ha is invariant with respect to species number, latitude or elevation, even though tree density increases from northern to southern latitudes (Fig. 1b–d). Likewise, species diversity has no effect on total standing biomass, although tree density rapidly asymptotes with respect to species diversity (Fig. 1e–f). Finally, as predicted by theory, the number of individuals per sample area scales as the  $-2$  power of stem diameter or as the  $-3/4$  power of body mass both within and across communities (Fig. 2). It seems as though both temperate and tropical forests are described by similar size distributions (Fig. 2a). Notably, the  $-2$  scaling rule also holds with increasing geographic sampling areas, including continental and global samples (Fig. 2). Latitude and



**Figure 1** Properties of tree-dominated communities. Solid lines are regression curves based on model type I regression analyses. **a**, Number of tree species per 0.1 ha plotted against latitude. **b**, Biomass (triangles) and number of trees per 0.1 ha (squares) plotted against latitude (negative values indicate degrees south) (regression of untransformed data for tree biomass and number against untransformed latitude:  $n = 220$ ,  $r^2 = 0.0024$ ,  $F = 0.5283$ ,  $P = 0.4681$  and  $n = 220$ ,  $r^2 = 0.2570$ ,  $F = 77.49$ ,  $P < 0.0001$ , respectively). Filled symbols denote data for communities from high elevations ( $\approx 1,200$  m), all of which are from low latitudes ( $\leq 20^\circ$  S and N). **c**, Number of trees per 0.1 ha plotted against latitude (see **b** for log-arithmetic plot of untransformed data). **d**, Number of trees per 0.1 ha (squares) and total standing tree biomass (triangles) plotted against elevation (regression of untransformed data against elevation gives

$n = 145$ ,  $r^2 = 0.0007$ ,  $F = 0.1063$ ,  $P = 0.7449$  and  $n = 141$ ,  $r^2 = 0.0004$ ,  $F = 0.052$ ,  $P = 0.820$  and  $n = 227$ ,  $r^2 = 0.4789$ ,  $F = 206.8$ ,  $P < 0.0001$ , see **f**; regression of untransformed data for tree biomass per 0.1 ha against species number gives  $n = 221$ ,  $r^2 = 0.0013$ ,  $F = 0.294$ ,  $P = 0.588$ ). Closed symbols denote data from high elevations ( $\approx 1,200$  m) or high latitudes (all high elevation plots are from low latitudes, that is,  $\leq 20^\circ$  S and N; see **b**). **f**, Number of trees per 0.1 ha plotted against species number per 0.1 ha (see **e** for log-arithmetic plot).

species number do not contribute greatly to the variance observed in local size distribution exponents ( $n = 226$ ,  $F = 50.05$ ,  $r^2 = 0.183$ ,  $P < 0.0001$  and  $n = 200$ ,  $F = 22.76$ ,  $r^2 = 0.092$ ,  $P < 0.0001$ , respectively) (Fig. 3a, b). Furthermore, neither the size–frequency distribution exponent nor the number of individuals is correlated with annual precipitation<sup>28,29</sup> ( $n = 91$ ,  $F = 0.893$ ,  $r^2 = 0.0099$ ,  $P < 0.347$ , and  $n = 91$ ,  $F = 2.545$ ,  $r^2 = 0.0278$ ,  $P < 0.1142$ , respectively).

Neither latitude nor elevation can serve as a surrogate measure of climate. Here, each is used simply as an independent variable against which to plot total tree standing biomass across communities differing in species composition as well as geography<sup>28,29</sup>. Likewise, the biomass reported here neither include trees smaller than 2.5-cm d.b.h. nor that contained in roots or nonarborescent vegetation (see Methods). For each community, however, the largest trees per site account for between 15% and 27% of the total standing tree biomass, whereas maximum tree size is invariant with respect to latitude ( $n = 225$ ,  $r^2 = 0.00001$ ,  $F = 0.0002$ ,  $P = 0.9896$ ) or species number ( $n = 226$ ,  $r^2 = 0.008$ ,  $F = 1.755$ ,  $P = 0.187$ ).

The principal exceptions in our findings are the size distributions for communities from high latitudes ( $\geq 40^\circ$  N or S). For these communities, the size distribution exponent tends to be less negative than  $-2$ , indicating lower densities of smaller individuals (see Figs 2 and 3). However, no significant correlation is observed between the exponent of the size frequency distribution and elevation ( $n = 144$ ,  $r^2 = 0.015$ ,  $F = 2.179$ ,  $P = 0.1421$ ). Clearly, one or more ecological features (for example, periodic recruitment, disturbance and/or length of the growing season) probably further limits the ability of individuals at the highest latitudes to fully occupy physical space. Yet even for these communities total standing biomass is, on average, indistinguishable from that of communities from lower latitudes or elevations, suggesting compensation by the largest individuals. Furthermore, with

increased geographic sampling area, high-latitude North American forests approximate the  $-2$  scaling rule (see Fig. 1, legend).

The available data for tree-dominated communities do not permit a direct test of our prediction that the rate of resource use and mass production in tree communities is invariant with respect to body size or species composition<sup>17</sup>. However, as (1) both total biomass and size–frequency distributions vary little with respect to latitude or tree species composition, and (2) a single allometric function describes interspecific rates of biomass production across all plants<sup>17,18</sup>, strongly suggesting this invariance across natural stands, the intrinsic capacities to use resources and to produce biomass per unit area may be equivalent.

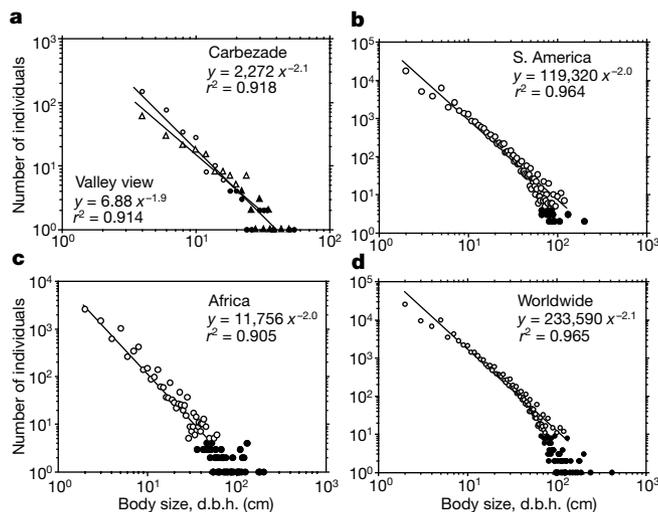
Variance in resource use and ultimately annualized rates of net primary production (NPP) across closed-canopy forest communities reflects the influence of many different ecological factors that reduce the capacity of metabolic production (for example, abiotic and biotic features of ecosystems that influence the extent to which plants can maximally transpire water and assimilate CO<sub>2</sub>; ref. 6) rather than variation in species diversity. This prediction is in accord with recent findings for North American herbaceous communities showing little relationship between empirical measures of NPP and plant species richness<sup>12</sup>. Similarly, gross primary production (of which NPP is an approximate constant fraction<sup>3,30</sup>) across European forests has been found to be invariant with latitude (a surrogate measure of species richness)<sup>31</sup>.

### An algorithmic model for community dynamics

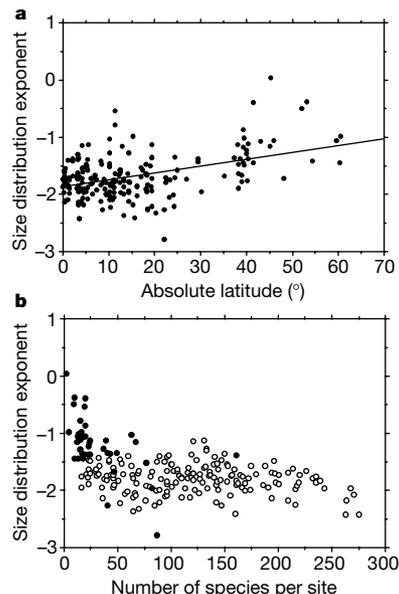
Likewise, when allometric theory is cast in terms of a simple algorithm for biomass allocation at the level of an individual plant, computer models predict that resource use will be invariant within and across monotypic and mixed tree communities. Moreover, all of the observed scaling relationships observed for real tree-dominated communities are predicted when the theory is cast in terms of a computer simulation model.

The conceptual basis for simulating the properties of real communities based on the allocation patterns of individual plants begins with a balanced energy formula

$$E_T - E_r = E_R + E_L + E_S \quad (3)$$



**Figure 2** Size–frequency distributions of forest communities differing in geographic sampling area<sup>8,9</sup> calculated for all size bin classes containing  $\approx 5$  individuals (open symbol) owing to the data display of statistically under-represented size classes (filled symbols). The 95% CI of the exponent for each distribution includes the predicted value of  $-2.0$  based on model type I or II regression analyses. **a**, Overlapping size–frequency distributions of a 0.1-ha sample of the South American tropical forest community located at Cabezade ( $-10.2^\circ$  latitude; data shown as open circles) and a 0.1-ha sample of a North American community located at Valley View Glades, Missouri ( $38.15^\circ$ ; data shown as open triangles). **b**, Pooled data for all South American forest 0.1-ha sample sites. **c**, Pooled data for all 0.1-ha samples of African forest sites (pooled continental data for the forested communities from Asia and North America also have exponents indistinguishable from  $-2$ ). **d**, Pooled data for all forest 0.1-ha samples represented in the data set (worldwide).



**Figure 3** Exponents of size–frequency distributions of forest communities. **a**, Exponents of each community plotted against absolute latitude. **b**, Exponents of size–frequency distribution of individual communities plotted against species number in each community (filled circles denote data from communities in high latitudes or elevations).

where  $E_T$  denotes the total light energy intake of an individual plant,  $E_r$  designates the energy consumed by respiration, and  $E_R$ ,  $E_L$  and  $E_S$  respectively denote the amount of  $E_T$  available for the construction of reproductive organs, leaves and stems, which differs across species comprising a particular community. In turn, the energy allocated to each of the three above-ground ‘compartments’ is converted into a biomass specified by the formula

$$aM_T^\alpha = bM_R^\beta + cM_L^\chi + dM_S^\delta \quad (4)$$

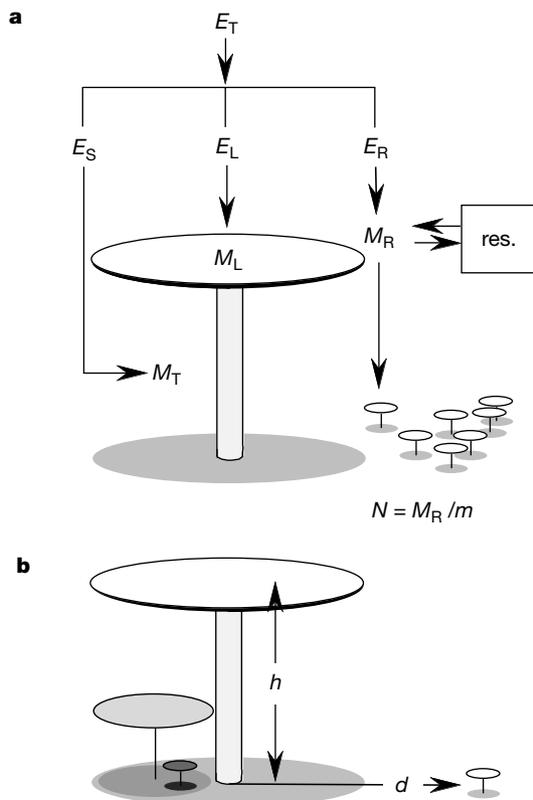
where  $a$ ,  $b$ ,  $c$  and  $d$  are constants of proportionality, and  $\alpha$ ,  $\beta$ ,  $\chi$  and  $\delta$  are species-specific scaling exponents among which the numerical value of  $\alpha$  is dependent on the numerical values assigned to  $\beta$ ,  $\chi$  and  $\delta$ . Within the model, species differ in values of  $a$ ,  $b$ ,  $c$  and  $d$ . For the purposes of this paper, theoretically predicted quarter-power exponents were used for all species<sup>14</sup>. Together, the magnitudes of  $b$ ,  $c$  and  $d$ , and  $\beta$ ,  $\chi$  and  $\delta$  determine biomass allocation patterns across species.

The balanced energy and mass formulas dictating allometric allocation patterns at the level of the individual (see equations (3) and (4)) were incorporated into a computer program designed to predict the consequences of competition for light and space. Each

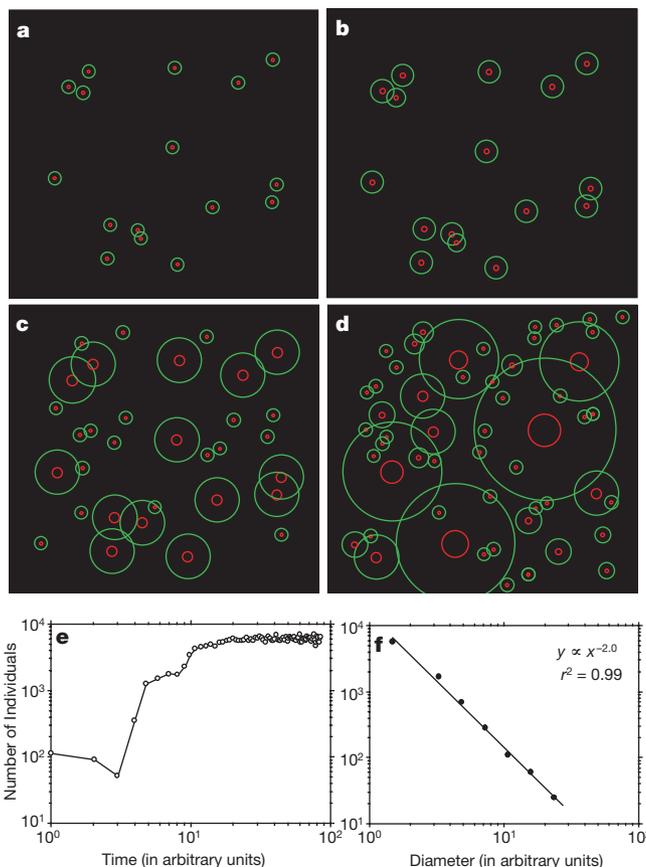
individual consists of a single vertical ‘trunk’ with height  $h$  and diameter  $d$ , which elevates a circular ‘canopy’ with radius  $r$  and height  $h$ . The height  $h$  of each individual is a function of the biomass allocation to the stem compartment. In each simulation (see below), the biomass allocated for the construction of leaves and stems is added to each ‘growing’ individual at the end of each time interval (Fig. 5).

All plants compete for spatially limiting ‘light’ resources on a world space, which is divided into a system of subgrids. The light energy available to each individual is calculated at each time interval. Each unobstructed canopy element receives 100% sunlight. Individuals located beneath the portions of successively overlapping (shorter) canopies receive proportionately less light energy (expressed as a percentage) defined by a predetermined canopy attenuation factor. This attenuation factor is equivalent for conspecifics but may in principle differ across species. Elements located over trunks receive no light energy.

Depending on its species assignment, an individual may use all or some of its metabolic production for the construction of its reproductive organs during each iterative time interval. In the former case, the total biomass of the  $n$  number of propagules produced at the end of each time interval equals  $M_R$ ; in the case of individuals reserving a portion of their  $M_R$  for subsequent use (that is, those that ‘reserve’ some or all of their reproductive effort), the total biomass of the  $n$  number of propagules produced at any



**Figure 4** Assumptions used to model biomass allocation among three above-ground plant compartments and stochastic features affecting dispersal and mortality. **a**, Species-specific assumptions. Total energy intake  $E_T$  is partitioned among three compartments (stem  $E_S$ , leaf  $E_L$  and reproductive effort  $E_R$ ) and converted per unit time into biomass (stem  $M_S$ , leaf  $M_L$  and reproductive effort  $M_R$ ) according to specified allometric ‘rules’. Some of the available reproductive biomass may be reserved for future use (res.); however, the total number of propagules produced at any time  $N$  is the quotient of the available reproductive biomass and the species-specific biomass of each propagule  $m$  (that is,  $N = M_R/m$ ). **b**, Dispersal and mortality assumptions: propagules are dispersed randomly to a maximum distance  $d$  defined by the height of the parent individual  $h$ . A propagule that begins growth under the canopy of one or more mature individuals receives less light, and, depending on its species-specific minimum light requirement and the species-specific light attenuation of the canopy, either dies or grows less vigorously.



**Figure 5** Results of representative simulations based on the assumptions of the model for biomass allocation (see Fig. 4). **a–d**, Partial polar views of four stages in the ‘ontogeny’ of a community, from the initial random ‘seeding’ of propagules (**a**) to the appearance of a ‘mature’ community consisting of a more or less constant number of individuals (**d**). Large green circles denote canopy radius; small red circles denote stem girth. **e**, Number of individuals plotted against time during the ‘ontogeny’ of a simulated community. **f**, Size–frequency distribution of a simulated community (number of individuals plotted against stem diameter) with a  $-2.0$  exponent calculated for all size bin classes (see Fig. 2).

time equals some portion of the biomass reserved over all previous time intervals.

A below-ground (root) compartment is not explicitly included in equations (3) and (4), largely because of the many uncertain assumptions required to emulate its metabolic demands, growth and energy-storage capacity. Conceptually, however, an equivalent fraction of the energy/biomass devoted to the construction of each of the three above-ground compartments can be thought of as diverted to the root compartment such that this 'sink' is implicitly treated and can be thought of as subsumed by the variable  $E_r$  in equation (3).

Among 'juveniles', death from light starvation is the result of extensive canopy overlap (that is, the probability of dying is determined by the light attenuation factor and the number of overlapping canopies above shorter individuals). In addition, for all individuals, there is a constant probability of death each time step independently of plant size (this probability can be specified, for example, as a stochastic process, or as a linearly or nonlinearly increasing probability defined as some function of the size of an individual). Seed dispersal is assumed to be passive and modelled according to the ballistic model<sup>12</sup>

$$\frac{d}{h} = \frac{u_s}{u_w} \quad (5)$$

where  $d$  is dispersal distance,  $u_s$  is the settling velocity of the seed (scaled as a function of its biomass, which in turn depends on the total biomass allocated to reproductive effort and how this biomass is subdivided among  $n$  number of seeds), and  $u_w$  is ambient wind speed measured at  $h$  (scaled according to different wind-speed profile formulas used to evaluate their effects). Seed size does not vary within species but can be made to vary across species.

When the allometry of biomass allocation at the level of an individual plant is expressed in terms of theoretically predicted quarter-power scaling functions<sup>14</sup>, the emulated 'ontogeny' of monospecific or mixed plant communities (Fig. 5a–d) obtains a typical sigmoid curve (Fig. 5e) and the scaling relationships  $N \propto D^{-2}$  and  $N \propto M^{-3/4}$  once the size–frequency distribution of a community reaches equilibrium (Fig. 5f). These scaling relationships become more statistically robust as the size (spatial sampling area) of the community is increased. Furthermore, the model predicts equivalent amounts of biomass across communities differing in species composition at equilibrium. These predictions are consistent with findings that the spatial scale of sampling influences the form of the relationship among the number of species per unit area, the number of individuals per unit area, and productivity<sup>12</sup>. Noting that the behaviour of simulated plant communities reflects a biomass optimization process operating at the level of individual plants, we conclude that the invariant properties identified for real plant communities emerge from the allometric rules that influence the behaviour of individual plants competing for space and limited resources.

### Ecological and evolutionary implications

Numerous studies show surprisingly little variation in the basic allometric relationships that define how different tree species occupy space, produce biomass, or apportion biomass among their body parts<sup>6,15,17,20–22,33</sup>. Therefore it is not surprising that our empirical and theoretical findings accord well with published data showing considerable numerical overlap in basal stem area, leaf area and carbon content per unit area among temperate and tropical forests<sup>3,5,28,34,35</sup>. For example, our analysis of additional larger compiled databases<sup>34</sup> indicates that total standing tree biomass (kg dry weight per 0.1 ha) varies little with respect to latitude across communities ( $r^2 = 0.028$ ,  $n = 827$ ,  $F = 23.81$ ,  $P < 0.0001$ ). Also, the total cross-sectional basal area of trees per 0.1 ha, which reflects the capacity of individuals to fill space, varies little with respect to latitude ( $r^2 = 0.029$ ,  $n = 715$ ,  $F = 20.96$ ,  $P < 0.0001$ ).

The assumptions of our allometric model and computer simulation are applicable theoretically to all vascular plant species<sup>36</sup>. With the exception of a small number of parasitic and hemiparasitic species, all tracheophytes compete for light and/or space. Likewise, all share the same basic body plan and must abide by the same general biophysical principles and processes<sup>36,37</sup>. Furthermore, across a broad sampling of diverse plant taxa (unicellular algae, pteridophytes, gymnosperms and angiosperms) biomass production is described by a single allometric relationship<sup>18</sup>. Theoretical plant morphology also suggests that land plant evolution was profoundly influenced by optimization processes required by the trade-offs necessitated by simultaneously performing manifold tasks essential for growth, survival and reproductive success. These trade-offs confined phenotypic expression to a finite number of morphologies<sup>38</sup>. Much evidence thus converges on the conclusion that communities dominated by plants behave similarly by virtue of shared organizing principles operating at the level of the individual.

A growing body of allometric and biomechanical evidence also strongly indicates that plant species have evolved diverse biomass allocation patterns that nonetheless abide by the same fundamental trade-off patterns. Indeed, when seen from an allometric perspective, many of the life-history differences across species reflect subtle (albeit biologically important) variants on a general theme whose mathematical structure is defined by the unavoidable necessity to reconcile conflicting functional design specifications<sup>14,36</sup>. For example, different species allocate different amounts of their annual metabolic production to reproductive effort. Yet, regardless of any particular metabolic or physiological allocation pattern, stoichiometric and allometric relationships influence the nature of biological trade-offs<sup>15–17,39,40</sup>. Trade-offs associated with allometric relationships constrain biomass devoted to reproductive effort and to vegetative growth, as a finite allometrically determined amount of metabolic production is available at any time<sup>15–17</sup>. By altering the timing of biological events, fundamental trade-offs facilitate the coexistence of several species and ultimately result in substantial variations in growth rate, lifespan and reproductive effort<sup>17</sup>.

### Discussion

We have shown that despite wide variation in species diversity, abundance and biomass, tree-dominated communities are characterized by nearly identical size–frequency distributions reflecting nearly equivalent standing biomass. We have also shown that the number of individuals in each community sample scales as  $D^{-2}$  and thus  $M^{-3/4}$ . These observations are consistent with allometric theory and with our computer model of biomass allocation but contrast in many important ways with past speculations and niche-based theoretical predictions<sup>4,10,11</sup>. Allometric theory suggests that variation in plant species composition is instead associated with concomitant changes in the degree of partitioning of a limited amount of resources rather than increases (or decreases) in community biomass and, potentially, depending on the local environment, productivity<sup>4,10–11</sup>. Such partitioning is most probably reflected in life-history trade-offs in the allocation of metabolic production<sup>17</sup>.

Extensions of a general allometric framework and simulation model reveal how several prominent organismal, community and ecosystem level properties emerge from relatively few allometric and biomechanical 'rules'. The constraints of resource transport through 'fractal-like' vascular networks ultimately dictate how individuals fill space, use resources and produce and allocate biomass<sup>14–18</sup>. Such constraints are reflected in allometric scaling relationships, which are evident at many levels in biology. These 'rules' dictate how metabolic production and biomass are partitioned among different body parts at the level of the individual plant. Furthermore, they provide a quantitative basis for drawing mechanistic connections between numerous features of organismal biology, ecology, ecosystem studies and evolutionary biology. □

Methods

Calculation of community biomass

To test our theory, we estimated the total standing above-ground biomass. We also determined the size (stem diameter) frequency distribution for all individuals from each site. The total standing (above-ground) tree biomass for each community was calculated from d.b.h. values using empirically determined scaling exponents and constants of proportionality reported in the literature for representative communities growing in latitudes and elevations equivalent to those communities in the Gentry data<sup>22</sup>. Data for trees of tropical dry, moist and wet forest indicate that the interspecific allometry is  $M = 0.124D^{2.53}$ , where  $M$  is measured in kg of dry (above-ground) biomass and  $D$  is in cm d.b.h. (ref. 22). The allometric proportionality constants and the exponents reported in the literature did not significantly vary between temperate and tropical forests<sup>15–17,20–22,33</sup>. Our allometrically estimated community biomass for both temperate and tropical sites per 0.1 is statistically indistinguishable from empirically determined biomass values for forests with similar minimal size cutoffs<sup>33,34</sup>. Nonetheless, we used different scaling exponents to evaluate their impact on estimates of total standing tree biomass. Our analysis showed that using different scaling exponents to estimate total standing biomass had no effect on the invariance of this parameter with respect to latitude or species number. This is because differences in estimated total community biomass remained constant across communities regardless of which scaling exponent was used (that is, the absolute magnitude of standing biomass was affected but not the relative differences across communities).

Community size distributions

Size class-bins were defined at 2-cm d.b.h. intervals and were then log-transformed. Each size–frequency distribution was characterized in terms of its  $y$  intercept and slope (scaling exponent) using both model type I and model type II regression analyses on log-transformed data. Regression analysis between the slopes obtained using model type I and II regression analyses indicates no significant difference in the scaling exponent ( $r^2 = 0.9728$ ). Model type I regression analysis was used when error estimates in  $x$  values were likely to be minimal (such as latitude, elevation and basal stem diameter (d.b.h.)). Model type II regression analysis was used to determine the allometric scaling exponents for variables neither of which could be assumed to be independent of one another (such as species number and total number of individuals per community)<sup>15</sup>. In most cases, because of high  $R^2$  values, the choice of which regression model has little or no effect on the scaling exponent. Size distribution exponents were calculated for sites where the tree size range exceeded 45-cm d.b.h.

Computer simulations

Simulations of plant community growth and dynamics were written in objective C and conducted on the SWARM simulation platform based in part at the Santa Fe Institute and developed by the Swarm Development Group. The basic architecture of Swarm is the simulation of collections of concurrently interacting agents (see <http://www.swarm.org/>).

Each simulation begins with a pre-selected number of ‘seeds’ randomly dispersed in a world-space of predetermined size. The seeds are either all conspecifics (to emulate the behaviour of a monotypic community), or are individually assigned a species-specific biomass, light requirement and dispersal range (to construct a mixed community). In either case, the ambient light intensity is uniform and invariant across all simulations (that is, all unobstructed surfaces receive 100% light energy).

The height  $h$  of each individual is a function of the biomass allocation to the stem compartment. Within the model height cannot exceed the critical Euler buckling height  $h_{crit}$ , which is proportional to the 2/3 power of stem diameter; specifically,  $h_{crit} = C(E/\rho)^{1/3}D^{2/3}$ , where  $C$  is a proportionality constant,  $E$  is Young’s modulus, and  $\rho$  is average stem-tissue density<sup>15</sup>.

Once a simulation is initiated, all species-specific parameters remain constant (that is, there is no genetic variation among conspecifics and thus no ‘evolution’). The time-interval designating the conversion of light energy into biomass is uniform and invariant among all simulations. Community properties such as the number of individuals, total standing biomass, size–frequency distributions (measured in terms of plant height, stem diameter, total biomass, and so on), and other statistical parameters can be retrieved at any time-interval without terminating the simulation.

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Supplementary information is available on Nature’s World-Wide Web site (<http://www.nature.com>) or as paper copy from the London editorial office of Nature.

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